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Summary. Within a relatively short geological time frame, Neolithic man, or more probably woman, domesticated all the major cereal grains, legumes, and root crops that the world's people depend on for most of their calories and protein. Until very recently, crop improvement was in the hands of farmers. The cornerstones of modern plant breeding were laid by Darwin and Mendel in the late 19th century. As the knowledge of genetics, plant pathology, and entomology have grown during the 20th century, plant breeders have made enormous contributions to increased food production throughout the world. There have been major plant breeding breakthroughs for maize and wheat, and promising research activities to raise yields in marginal production environments are ongoing. Since it is doubtful that significant production benefits will soon be forthcoming from the use of genetic engineering techniques with higher plants, especially polyploid species, most research funds for crop improvement should continue to be allocated for conventional plant breeding research.

In 1979 world food production of all types reached 3.75 billion metric tons, representing 1.9 billion tons of edible dry matter. Of this dry matter tonnage, 99 percent was produced on land; only slightly more than 1 percent came from oceans and inland waters. Plant products constituted 93 percent of the human diet. The remaining 7 percent of the world's diet, animal products, also came (indirectly) from plants.

Archeological evidence indicates that more than 3000 species of plants have been used by man for food. Currently, the world's people largely depend on about 29 crop species for most of their calories and protein. These include eight species of cereals, which collectively supply 52 percent of the total world food calories, three "root" crops, two sugar crops, seven grain legumes, seven oil seeds, and two so-called tree food crops (bananas and coconuts). These 29 basic food crops are supplemented by about 15 major species of vegetables and a like number of fruit crop species, which supply much of the vitamins and some of the minerals necessary to the human diet.

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Origin of Food Crop Species and Early Genetic Improvements

We will never know with certainty when nature first began inducing genetic diversity, making recombinations, and exerting selection pressure on the progenitors of the plant species that would be chosen, much later, by man as his food crop species. But as the Mesolithic Age gave way to the Neolithic there suddenly appeared, in widely dispersed regions, the most highly successful group of plant and animal breeders that the world has ever seen—the Neolithic domesticators. Within a relatively short geological period, apparently only 20 to 30 centuries, Neolithic man, or more probably woman, domesticated all of the major cereals, grain legumes, root crops, and animal species that remain to this day as man's principal sources of food.

Agriculture and animal husbandry spread rapidly from their cradles of origin across vast areas of Asia, Africa, Europe, and the Americas. These migratory diffusions were in large part possible because of the tremendous genetic diversity that existed in the original land races and populations of the domesticated crop plants. This genetic variability permitted—with the aid of continued mutations, natural hybridizations, and recombinations of genes—the spinning off of new genotypes that were suitable for growing in many environments.

Golden Age of Plant Breeding

Until the 19th century, crop improvement was in the hands of farmers who selected the seed from preferred plant types of land races or populations for subsequent sowing. By the early decades of the 1800's, a number of progressive farmers in North America were busy developing and selling superior varieties based on individual plant selections.

The groundwork for genetic improvement of crop plant species by scientific man was laid by Darwin in his writings on the variation of life species (published in 1859) and through Mendel's discovery of the laws of inheritance (reported in 1865). While Darwin's book immediately generated a great deal of interest, discussion, and controversy, Mendel's discovery was largely ignored at first. Nearly 40 years transpired before these two strands of scientific thought were joined by Karl Correns, Erich Tschermak, and Correns De Vries in independent studies. This rediscovery of Mendel's laws in 1900 provoked a tremendous scientific interest in genetics. The fact that Mendel had worked out his principles on a plant (the sweet pea) encouraged many to prepare themselves for a career in applied plant genetics.

Methods Used in Modern Plant Breeding

The three major categories of plant breeding research are divided on the basis of how various species propagate themselves. Species that reproduce sexually and are normally propagated by seeds—including all cereal crops, legumes, and most trees and shrubs—occupy the first two categories. One of these includes species that set seed through self-pollination; the second, species that set seed largely through cross-pollination. The third category includes species that are asexually propagated through the planting of vegetative parts or grafting. In this article I mainly discuss plant breeding achievements in wheat, a self-pollinating species, and maize, a cross-pollinating species.

The cornerstones of all plant breeding are (i) the conscious introduction of genetic diversity into populations by intercrossing or mating selected germ plasm with outstanding characters that complement one another and (ii) the selection of superior plants with genes for desired traits until higher levels of improved adaptation (reproductive fitness), genetic uniformity, and agronomic stability are reached. The appropriateness of a breeding methodology is determined mainly by the sexual nature of the crop—inbreeding (self-pollinating) or outbreeding (cross-pollinating)—its genetic structure, and the objectives to be achieved.

Wheat Breeding

As the knowledge of genetics and plant pathology grew during the first and second decades of this century, wheat breeding methods evolved from bulk and pure-line selections of plants from land races to hybridization programs. With this methodology, controlled pollinations are made between two or more superior parent types. In subsequent segregating generations derived from these controlled crosses, the individual plants possessing the best combinations of desirable characteristics are selected and advanced to the next generation. This process is repeated until all progenies from an individual plant row are genotypically and phenotypically uniform. When acceptable uniformity has been attained, the best progenies (lines) are sown in replicated multirow plots and compared with the best commercial varieties for grain yield, agronomic type, disease and insect reaction, and milling and baking quality. The trials are repeated for several years at a number of different locations to obtain reliable information on the interaction of the variety (genotype) with different environments. When a new line or variety has significantly outperformed existing commercial varieties over several years, it is eligible for multiplication and release as a new commercial variety.

As a result of such breeding techniques, a number of major breakthroughs in wheat breeding have occurred during the past four decades. Most significant among these include the progress made in plant pathology research to develop disease-resistant varieties, achievements in raising maximum genetic yield potential, and the benefits derived from broader adaptation in wheat crop cultivars.

Disease resistance. The pioneering work on stem rust by E. C. Stakman in Minnesota during 1913 to 1930 revealed that the rust organism comprises a large number of pathogenic races that differ in their ability to attack wheat varieties. This discovery led to the understanding that, for a wheat variety to maintain its resistance to stem rust, it had to possess resistance to all the races present throughout the region. With this greater understanding of pathogenic organisms, breeders began to develop more stable sources of genetic resistance in different wheat cultivars. Today, many improved wheat varieties have been developed that possess far broader spectrums of polygenic resistance to many of the 30 wheat diseases that can and do cause serious economic losses in different parts of the world.

Yield potential. Until about 1961 there was no significant increase in grain yield directly attributable to the increase in the maximum genetic yield potential of new varieties. The release of the first semidwarf winter wheat variety, Gaines, in Washington State by O. A. Vogel and his colleagues in 1961, followed by the release in Mexico of two semidwarf spring wheat varieties, Pitic 62 and Penjamo 62 in 1962 and Sonora 64, Lerma Rojo 64, Super X, and Siete Cerros in 1964, changed the potential wheat yield situation dramatically. The semidwarf varieties, all with one or two dwarfing genes derived from the Japanese winter wheat variety Norin 10, possessed a 100 percent yield advantage over the best previously available tall commercial varieties. Compared to the taller types, semidwarf varieties have a higher tillering capacity, more grain-filled heads, and shorter stems that make them resistant to lodging under higher levels of fertilization and irrigation. Perhaps even more important, however, was the change in the "harvest index" of semidwarf varieties to partitioning more of the total dry matter production to grain. As such, semidwarf varieties convert a higher percentage of the uptake of fertilizer and soil moisture to grain than do the taller types.

Adaptation. Until the 1950's, the dogma in plant breeding was that the only way to ensure the development of high-yielding, well-adapted varieties is to select them through all the segregating generations in the location where they are to be grown commercially. Faced with the urgent need to develop acceptable stem rust–resistant varieties in Mexico, a decision was made to ignore dogma and use several ecological areas that would permit the growing and selecting of two segregating generations of progeny each year. With two breeding cycles every 12 months, a new variety could be developed in 4 years rather than in the 8 years required with the conventional methods. To accomplish this task in a 12-month period, we at the International Maize and Wheat Improvement Center (CIMMYT) were forced to select two very diverse environments separated from one another by 10° of latitude (with changing day lengths) and differing in elevation by 2600 meters. Segregating populations were shuttled, grown, and selected in these two very different environments. Only varieties that withstood the rigors of both environments were advanced in the breeding program.

The results were startling. Not only did these varieties yield well in Mexico, they also performed well in many other environments, from Canada to Argentina, because of their more general insensitivity to differing day lengths. In contrast, U.S. and Canadian varieties performed well only in the areas where they were developed. The development of these broadly adapted spring wheat varieties not only benefited Mexico, but later had a tremendous impact on wheat production in other parts of the world.

Maize Breeding

In the 19th century American farmers made important varietal improvements in the maize species by continuously reselecting the best ears from the best plants in open-pollinated varieties and regrowing them the following year. The introduction of seed from diverse maize-growing areas resulted in natural hybridization with local cultivars. Natural crossing and subsequent mass selection activities gave rise to the open-pollinated dent varieties of the U.S. Corn Belt. These varieties continued in use until the development of hybrids.

Development of F_1 hybrids. It was recognized early on that inbreeding in maize leads to reduced vigor in the following generation and that vigor can be restored by crossing. Darwin noted this phenomenon in *The Vegetable Kingdom*, published in 1876. The first organized attempt to exploit hybrid vigor in maize was initiated by W. J. Beal at Michigan State College in 1875. Beal's work and that of others stimulated little interest for 25 years until Edward East and George Schull proved conclusively that although maize lost vigor on inbreeding, when inbred lines were crossed, the progeny of the next generation exhibited an explosive recovery of vigor called heterosis. The problem that remained was how to exploit the heterosis commercially, since the cost of F_1 hybrid seed would be prohibitively expensive.

The solution was forthcoming from the work of Donald Jones, who had joined East's staff in 1915. In 3 years he found a solution to the high "seed cost" of producing hybrids, and in the process increased yields above those of the original single-cross hybrids. His approach was to mate two single-cross hybrids, formed by intercrossing four inbred lines, to produce what is called a double-cross hybrid. This was a giant step toward solving the problem of reducing the cost of hybrid seed to the farmer.

But there was no stampede to exploit this potential until the mid-1920's, when H. A. Wallace, later to become Secretary of Agriculture and Vice President under Roosevelt, founded Pioneer, Inc., the first private hybrid seed company. Because of the disastrous economic depression of the 1930's, the use of hybrids did not really take off until the early 1940's. But by the mid-1950's hybrids dominated U.S. maize production and the use of open-pollinated varieties had virtually disappeared.

Since the commercial introduction of the first hybrids in the United States some 40 years ago, many improved elite hybrids with continually higher yields, improved disease and insect resistance, and shorter and stronger stalks suitable for mechanical harvesting have been developed.

Open-pollinated varieties. Efforts to improve maize yields in the developing world have not achieved the spectacular successes characterized by hybrid maize production on the well-watered soils of mid-America. For reasons related to the economic circumstances of farmers and the nascent agricultural infrastructure of most developing countries, the CIMMYT breeding program has focused on developing superior open-pollinated populations and varieties to serve the special needs of Third World countries. More than 24 populations have been developed that can serve the major environmental, maturity, and grain requirements of the developing world. For more than a decade, these populations have been improved by recurrent selection through a multilocational international testing system for yield potential, disease and insect resistance, grain type, and various agronomic characteristics. Some 70 open-pollinated varieties derived from these populations have been released by national breeding programs in over 20 developing countries. These open-pollinated varieties are surpassing traditional Third World varieties in yield potential by 20 to 35 percent and have better agronomic characteristics and earlier maturity.

Certain of these improved populations also maintain their yield superiority (and dependability) over a very wide range of environments. It has now become clear from the dynamic recurrent selection program carried out at multilocational sites that it is possible to breed high-yielding, open-pollinated varieties with a broad spectrum of disease and insect resistance that can, at the same time, have an amazingly broad adaptation across many latitutdes and elevations.

Table 1. Impact of improved technology on land use, crop yield, and production in the United States.

Crop	Area (thousands of hectares)	Yield (tons per hectare)	Production (thousands of tons)
	1938 to 1940		
Maize	36,014	1.80	64,104
Wheat	23,635	0.96	22,453
17 major crops*	128,820		252,033
	1958 to 1960		
Maize	29,714	3.36	99,891
Wheat	21,419	1.67	35,883
17 major crops	127,436		391,388
	1978 to 1980		
Maize	29,338	6.32	185,208
Wheat	25,614	2.22	57,016
17 major crops	132,544		610,293

*Corn, wheat, rice, barley, sorghum, oats, rye, cotton, soybeans, peanuts, beans, flaxseed, potatoes, sugar beets, hay, corn silage, tobacco.

Improved nutritional quality. The discovery in 1964 at Purdue University that the mutant opaque-2 gene increases the lysine and tryptophan content of maize by more than 50 percent created considerable excitement among many agricultural scientists and nutritionists. These are the two most limiting essential amino acids in maize for monogastric animals and man. Consequently, it was visualized that it would soon be possible to develop high-yielding maize materials with much-improved nutritional value. However, the difficulty of this task soon became apparent. When the opaque-2 gene was incorporated in maize materials it brought along a host of adverse effects, including a reduction in yield of 15 to 20 percent; a dull, soft, chalky kernel; increased susceptibility to ear diseases and to insects when in storage; and a slower drying rate of grain at physiological maturity.

While many maize breeders soon abandoned their work on opaque-2 maize, CIMMYT persisted in its attempts to develop nutritionally superior maize types with high yield potential and suitable grain and agronomic characteristics. A breakthrough was achieved with the discovery that "normal" maize populations have minor "modifier" genes that can influence the soft texture of the opaque-2 endosperm. A closely coordinated effort to overcome these defects was launched by two CIMMYT scientists and a biochemist. Through the development of a recurrent selection and backcrossing breeding scheme and rapid laboratory screening methods for protein quality, they were able to retain the high levels of lysine and tryptophan associated with the soft-textured opaque-2 endosperm, while pyramiding suitable modifier genes to convert the soft-textured materials to normal maize types with a hard-endosperm.

This conversion was done against the background of the best broadly adapted "normal" CIMMYT populations, so parallel improvements have been carried on for other characteristics simultaneously. The most advanced of the hard-endosperm protein maize materials have been evaluated internationally at a number of locations over the past 2 years. They have been found to be roughly equal in yield, in resistance to disease and insects, and in breadth of adaptation to the best normal varieties included in the yield trials.

Contributions of Plant Breeding to World Food: Wheat and Maize

The contributions of plant breeding research must be seen in the context of total research efforts to improve the effectiveness of agricultural production. Plant breeding, or genetic improvement, is but one element in a research triad that includes improvements through more effective crop husbandry and agronomic practices as well as more productive interactions between particular environments and genotypes.

During the 1940's the research components needed for high-productivity agriculture began to be applied in the United States and yield levels started their take-off, which continues today. The most spectacular increases, however, took place during the 1950's, 1960's, and 1970's with the rapid expansion of the infrastructure for the production and distribution of seed, fertilizers, herbicides, pesticides, and machinery.

Between 1940 and 1980 the combined production of 17 major crops in the United States increased 242 percent, from 252 million to 610 million metric tons (Table 1). This large increase in production was obtained with an increase in the area of cultivated land of only 3 percent. Had 1940 yield levels persisted in 1980, 177 million additional hectares of good U.S. cropland would have been needed to equal the 1980 harvest.

Table 2. Wheat production in India before and after the wheat revolution. [Data from the Indian national wheat program. Format adapted from that of B. A. Krantz]

Years	Wheat production (millions of tons)	Gross value of increase* (millions of dollars)	Number of adults provided with carbohydrate needs by increase† (millions)
1966 to 1967	11.39	88	3
1968 to 1969	18.65	1540	50
1970 to 1971	23.83	2576	94
1972 to 1973	24.74	2758	101
1974 to 1975	24.10	2630	96
1976 to 1977	29.08	3626	133
1978 to 1979	35.51	4912	180
1980 to 1981	36.50	5110	186

*The wheat value used is $200 per ton, similar to the landed value imported wheat in India in 1981. †Calculations are based on the provision of 65 percent of the carbohydrate portion of a diet containing 2350 kilocalories per day, or 375 grams of wheat per person per day.

The most impressive change in U.S. crop yields and production during the past 40 years has occurred with maize. Yields have increased 251 percent, due in large part to the introduction of high-yielding hybrids. A conservative estimate is that heterosis in hybrid maize contributed at least 20 percent to the 1980 harvest of 185 million metric tons. This was an increased production in 1980 of 37 million tons, worth approximately $4.5 billion in additional maize sales over what would have been achieved with the best open-pollinated varieties. As a result of the introduction of the new maize technology, 6.7 million fewer hectares were needed for maize production in 1980 than in 1940. Major yield increases in wheat and many other crops have also been achieved in the United States.

Beginning in the mid-1960's, improved agricultural technology began to reach the developing world as well. The establishment of the 13 international agricultural research centers over the past two decades has been a major factor in stimulating agricultural research on the major food crops and farming systems in the developing world. The most impressive achievements to date have been in wheat and rice. The plant breeding efforts of scientists at the International Rice Research Institute in the Philippines and CIMMYT in Mexico did much to avert the spectre of famine in Asia in the 1960's and 1970's.

In India the introduction of high-yielding wheat and rice varieties, in combination with improved agronomic practices that permitted these varieties to express their high genetic yield potential, has had a major impact on transforming food production.

When high-yielding semidwarf varieties of Mexican wheat were introduced into India during 1966 to 1968, national production stood at roughly 11 million metric tons and average yields were less than 1 ton per hectare (Table 2). The high-yielding wheat varieties quickly took over, and by 1981 wheat production had increased to 36.5 million metric tons, largely as a result of a 100 percent improvement in national wheat yields. The 1981 harvest increase of 25.5 million tons over the 1966 harvest represents sufficient additional grain to provide 186 million people with 65 percent of the carbohydrate portion of a diet containing 2350 kilocalories per day.

Equally impressive wheat production gains have been achieved in Argentina, China, Pakistan, Turkey, and, more recently, in Bangladesh. Total wheat production in developing countries has more than doubled over the past two decades. Although it is difficult to quantify the individual impact of the various components of production because of their interactions, certainly the use of high-yielding varieties developed through conventional plant breeding research, in combination with the increasing use of fertilizers and irrigation, has been a decisive factor in the increasing yields.

More recently, we are seeing the potential for major technological improvements in other vitally important food crops in the developing world. For example, data on maize production over the past two decades in the developing countries reveal that the average annual rate of yield increases in the 1970's was twice the rate achieved in the 1960's. This marked change, I believe, points to the beginning of a technological turning point in Third World maize production in the decade ahead. Given the importance of maize as a food and feed grain, and considering its relatively higher maximum genetic yield potential among the cereals, significant productivity gains will play a pivotal role in future world food production efforts.

The Next Doubling: Feeding 8 Billion People

World population growth dictates in large measure the increases needed in food production. Since the beginning of agriculture, world population has increased more than 256-fold (eight doublings), and now stands at approximately 4.5 billion. The challenge just to maintain already inadequate per capita food consumption levels is awesome. It took roughly from 12,000 B.C. until about 1850 for world population to reach 1 billion, only 80 years to reach 2 billion, and only 45 years to reach 4 billion. We are now faced with the need to double the world food supply again by the first decades of the 21st century.

The dramatic increases in yield that have occurred in American agriculture since 1940 through the introduction of science-based technology also indicate the long gestation period between the initiation of research programs and the application of results on a large scale. In the case of plant breeding, more than 50 years elapsed between initiation of the original genetic research and the time when the application of research results began to affect production significantly. The magnitude of the food production tasks ahead requires that we find ways to speed up this process of applying and diffusing research results.

The significance of increased crop production in the more marginial agricultural areas is an especially important dimension in feeding future generations. Some 600 million people live in the semiarid tropics and more than 1 billion live in tropical and subtropical areas characterized by serious biological constraints. I must caution that agricultural research alone cannot produce miraculous improvements in many of the more marginal production areas. Some of the biological limitations are simply too overpowering for science to currently overcome. Still, we can put science to work on a number of the problems faced in marginal land areas.

Future Plant Breeding Research Priorities

In some scientific circles today it is anticipated that major production benefits will soon be forthcoming from the use of genetic engineering. The new techniques in tissue culture, cell fusion, and DNA transfer are all being heralded as the scientific answers to increasing the breadth, level, and stability of disease resistance; eliminating the need for conventional chemical fertilizers; and further raising the genetic yield potential of food crops.

Although great progress has been made by employing genetic engineering techniques with bacteria or yeasts to increase the production of insulin and interferon, there is no firm evidence that similar results will be obtained with higher plants, especially polyploid species such as wheat. It will probably be many years before these techniques can be successfully used to breed superior crop varieties. Furthermore, it is a mistake to assume that the transfer into crop species of disease- and insect-resistant genes through genetic engineering will result in substantially more durable varieties than we have been able to achieve to date. Pathogens and insects, when faced with extinction, mutate into new races capable of attacking the resistant variety. This biological reality will continue to hound mankind in the years ahead.

Although some research funds should be directed toward the development of genetic engineering techniques to improve breeding programs, I believe that most of the research funds for crop improvement should continue to be used for conventional plant breeding research. There is much that remains to be done, and can be done, to further improve disease and insect resistance, enhance tolerance to environmental extremes, and increase genetic yield potential by employing conventional plant breeding methods.

At CIMMYT, increasing attention is being focused on the problems of marginal production areas. Two major breeding approaches are being pursued. One involves conventional breeding procedures in search of genetic variation in a particular crop species for added tolerance or resistance to specific agroclimatic and soil stress conditions. Improved genetic materials—in terms of drought, cold, and heat resistance and tolerance to mineral toxicities such as those found in saline and acidic soils—are emerging from this work. As one example, wheat researchers have identified materials with significantly greater tolerance to acid soils characterized by aluminum toxicity. Aluminum-tolerant wheat lines, developed in cooperation with Brazilian scientists, are showing extraordinarily high yield levels under this soil-stress situation. There are millions of hectares of potential wheat land with acid soils high in soluble aluminum that now can be brought into much higher yielding production.

Wide crosses between plant species are also being explored to transfer useful genes for added environmental stability in major crop species. Triticale—a hybrid of wheat and rye—is an example of research efforts that led to the development of a new crop species. In just two decades, tremendous strides have been made in increasing yield potential and improving agronomic types of triticale. Triticale yields have doubled and now are similar to those of the best bread wheats in optimum production environments. Triticale probably has a higher genetic grain yield potential than bread wheat because of its greater production of dry matter. Its strong production advantage over wheat is most evident in certain marginal areas characterized by cool temperatures, acid or sandy soils, and heavy disease pressure. In such environments triticale has shown a substantially higher yield advantage over wheat.

Research to cross domesticated species with related wild species is another promising research avenue that may lead to the development of varieties with greater yield potential and dependability in a number of important marginal areas. Generally, such wide crosses involve the breaking down of natural barriers between plant species in order to introduce useful genes from alien genera into domesticated crop species. We have identified a number of wild species with greater resistance to certain diseases and insects and tolerance to salinity, temperature, and moisture stresses than we have found to date in the germ plasm of the major crop species. Successful introgression of these desirable genes can lead to crop varieties with greater tolerance to environmental stresses.

I am convinced that the 8 billion people projected to be living 40 to 50 years from now will continue to find most of their sustenance from the same plant species that supply most of our food needs now. Fortunately, we still have large amounts of exploitable yield potential on which to capitalize, especially in the developing world, where eight of every ten new births occur. It is in these areas of the world where it is imperative to close the gap between actual and potential crop yields. We must also continue to work aggressively to raise average yields in the developed nations. Such yield increases will be more difficult to achieve as the maximum genetic yield of each crop species is approached.

New techniques, such as tissue culture and genetic engineering, offer potentially great payoffs and merit research resources in the years ahead. However, we should not neglect the more conventional areas of plant breeding research, since they represent the major line of defense today on the food front.